

Shark skin: a function in feeding

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Dermal denticles are unique tooth-like structures embedded in the skin of sharks and rays that protect them from predators and ectoparasites, reduce mechanical abrasion and possibly minimize swimming-induced drag. Here, we show that juvenile lesser spotted dogfish (*Scyliorhinus canicula*) also use this body armour to anchor food items near their tail so that bite-sized pieces can be torn away by rapid jaw and head movements. This scale-rasp behaviour is novel among fishes and suggests a new role for skin in the feeding ecology of sharks. Scale rasping may be important ecologically because it could function to increase the dietary breadth and growth potential of juveniles.

Keywords: dermal denticles; food processing; elasmobranch; ecomorphology

1. INTRODUCTION

The feeding strategies of fishes are diverse, ranging from filter-feeding and grazing forms to predators that swallow prey whole (Gerking 1994; Bone *et al.* 1995). Scavenging on the carcasses of dead animals is also a dominant feeding behaviour among fishes across habitats from the continental shelf (Long & Jones 1996) to the deep sea (Priede *et al.* 1991; Jones *et al.* 1998). However, predatory species that are gape limited with respect to prey size cannot swallow oversized food intact, so these species typically remove pieces using sharp teeth and jaw musculature (Long & Jones 1996). This presents a particular problem to juvenile stages because compared with adults they may be unable to generate the large biting forces necessary to pull apart firm prey. Moreover, there is the inherent problem for aquatic feeders lacking forelimbs of how to manipulate prey in a relatively weightless environment to create the opposing forces needed to tear prey into pieces.

The body surfaces of all 900 or so species of Elasmobranchii (sharks, skates and rays) are covered, to varying degrees, by dermal denticles (placoid scales) that have a plate-like base supporting a main body composed of dentine with an enameloid capping (Raschi & Tabit 1992). These denticles have undergone modification to form fin spines, flattened scales and teeth on the jaws (Bone *et al.* 1995). The functions of dermal denticles include protection from predators and ectoparasites, reduction of mechanical abrasion, accommodation of bioluminescent and sensory organs, reduction of frictional drag (Bone 1975; Reif & Dinkelacker 1982; Raschi & Tabit 1992; Ball 1999), and, in the case of oviparous sharks, facilitate the exit from the egg case (Ford 1921; Grover 1974). However, dermal denticles are not known to have a role in prey

processing or feeding behaviour. In this paper, we describe a novel behaviour in lesser spotted dogfish (*Scyliorhinus canicula*) that identifies dermal denticles as structures with a function in feeding.

2. MATERIAL AND METHODS

S. canicula hatched from eggs laid by wild-caught females were reared in laboratory aquaria at the Marine Biological Association and fed two or three times per week on finely chopped squid mantle muscle. At intervals over a period of seven months the feeding behaviours of 44 hatchling and juvenile *S. canicula* (age range of 10 days–15 months; body mass range of 1.9–70.7 g) were videotaped during trials where they were presented with squid pieces less than or exceeding their maximal mouth-gape area (gape area range of 50–380 mm²). Rectangular, oversized pieces of squid were scored with a knife along two sides to enable dogfish to seize the food item easily. Videotaped sequences of feeding behaviour were digitized (Pinnacle DV500 Plus, Pinnacle Systems Inc., USA) and analysed frame-by-frame to characterize different behaviour types and to determine the timing of particular activity patterns (ADOBE PREMIERE v.6, ADOBE Systems Inc., San Jose, CA, USA).

To investigate the roughness of dogfish skin, samples were taken from three dogfish aged between three and seven months in three lateral-body positions (head, anterior to the gill slits; middle, above and anterior to the pelvic fin lead-edge emargination; caudal, below and anterior to the second dorsal fin). These individuals were monitored during behavioural studies prior to skin sampling *post mortem*. Skin samples were prepared for scanning electron microscopy using standard procedures: fixation in 5% glutaraldehyde in seawater, secondary fixation in 1% osmium tetroxide in seawater, dehydration in acetone and critical-point drying. Scanning electron microscopy images were taken for measurements of denticle length (horizontal distance from the anterior cusp emargination to the cusp tip) and vertical extension (the cusp tip to the skin surface) of each individual in each of the body regions.

3. RESULTS

Microscopical examination of the dogfish skin revealed that 3–7-month-old individuals possessed numerous, well-defined dermal denticles in the lateral region (figure 1a). Generally, the length of denticles increased caudally, although the vertical extension from the skin surface varied little from anterior to posterior (table 1). In the lateral-caudal area, the mean length of denticles ranged from 0.43 to 0.68 mm and the mean vertical extension from 0.15 to 0.29 mm (table 1).

Behavioural analysis showed that dogfish used rapid head shaking and biting to break up prey prior to consumption, but this was only effective with small pieces of flesh (area of 25 mm²). With large squid pieces (area of 100–3600 mm²) that exceeded the maximal mouth-gape area, we observed dogfish of all ages conduct a consistent behaviour pattern that we term ‘scale rasping’ ($n = 323$ events in 52 feeding bouts, where a bout is defined as the responses of a number of fishes to food items presented at a specific time on one particular day). Scale-rasping behaviour was characterized by fishes making a rapid turn of the head towards the caudal area followed by prey manipulation and an even faster return flick of the head.

We analysed 22 videotaped scale-rasp sequences in detail. A typical scale-rasp sequence commenced with a dogfish seizing a large piece of squid in the jaws and swimming for between 5.6 and 40.2 s. After this initial phase the head was turned rapidly towards the lateral caudal-peduncle region below the second dorsal fin (mean $0.43 \text{ s} \pm 0.04 \text{ s.e.m.}$; $n = 16$ fish) (figure 1a,b). This head turning resulted in the food item making contact with the body whereupon it was squeezed between the mouth and the caudal region by two movements lasting *ca.* 0.34 s ($\pm 0.04 \text{ s.e.m.}$). The combined movements consisted of the following:

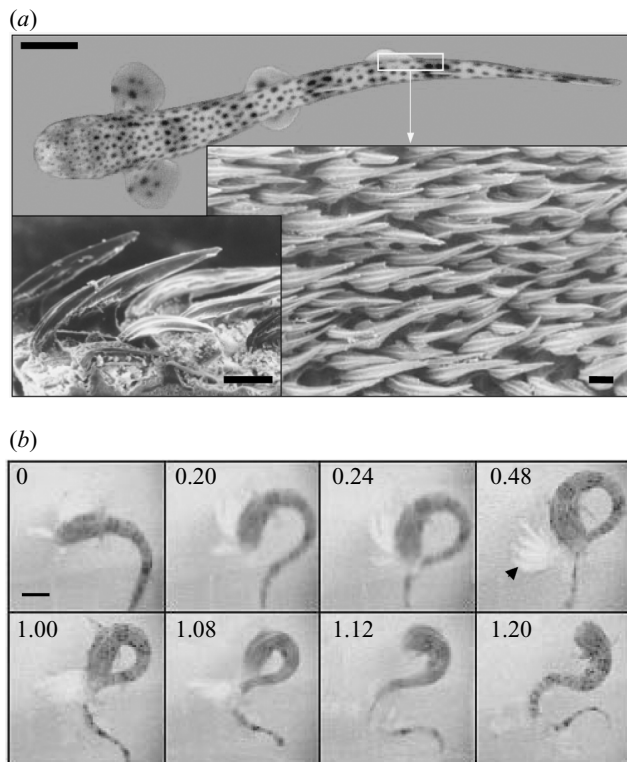


Figure 1. (a) Morphology of dermal denticles in the lateral-caudal region of a juvenile dogfish (white rectangle). The scale bar is 10 mm. First inset, surface view of the denticles; second inset, transverse view of the denticles illustrating their extension above the skin surface. Scale bars, 200 μ m. (b) Temporal sequence of the scale-rasp behaviour in a six-week-old dogfish of body mass 3.2 g. The number in each frame refers to the elapsed time (in s). Scale bar, 10 mm. The food mass is denoted by the arrowhead.

- (i) the tail curving backwards and outwards towards the food, producing a 40° bend in the tail between the first and second dorsal fins, where prey was positioned; and
- (ii) the head sliding anteriorly along the lateral body surface (figure 1b; frames 0.48 and 1.00 s).

These movements resulted in food becoming 'hooked' on prominent posterior-pointing denticles and in the prey being pulled taut (figure 1a,b). Immediately following this food-anchoring phase, the head was flicked in the return direction (cranially) at speeds approaching 40% faster than initial posterior head turning (figure 1b; frames 1.08–1.20 s). This head flick was observed to tear off a mouth-sized piece of food from the main mass. During the next 0.7 s normal swimming resumed and the small item was swallowed. The entire behaviour lasted *ca.* 1.6 s.

There was no right-left difference in the frequency with which food was approached immediately prior to food seizure (χ^2 test; $\chi^2 = 0.02$, $\chi^2_{0.05,1} = 3.84$, $p > 0.50$). Similarly, the frequency of right and left-oriented scale rasps was not significantly different from a 1:1 ratio (χ^2 test; $\chi^2 = 0.26$, $\chi^2_{0.05,1} = 3.84$, $p > 0.50$). Dogfish turned almost exclusively to conduct scale rasps on the side of the body closest to the food item (98.5% of events).

4. DISCUSSION

Our observations show that juvenile dogfish use dermal denticles for external manipulation and processing of food. They attach food in the lateral-caudal body region where denticles are longer than in other lateral regions. Dogfish used a rapid head jerk that moved anteriorly away from the posterior denticle-snagged food to create the opposing force necessary for a small piece grasped in the jaws to be removed from the main mass. The function of this behaviour in feeding was further confirmed by the lack of lateral preference for scale rasping by dogfish; rather, the side of the body chosen to rasp food was that closest to the item.

We found that scale rasping could be induced in dogfish by providing large, firm pieces of squid mantle muscle. However, not all sequences examined in detail ended with food being consumed. For example, one juvenile conducted three scale-rasp behaviours in 54.6 s but did not tear off any pieces and finally dropped the food mass after 74 s. In about one-third of the cases failure resulted from the food mass becoming detached from the denticled caudal area just prior to the return (anterior) head flick. Therefore, it seems that the success of dogfish using their body armour to brace prey against a tearing movement depends on how well the prey is anchored.

Sharks such as dogfish are known to reduce food in size by rapid head shaking and by repeated sucking and spitting of prey into and out of the mouth (Motta & Wilga 2001). However, to our knowledge, our study is the first observation of body surface being used by a fish species to help process food. The fact that newborn dogfish exhibited scale rasping suggests it is a programmed activity pattern. Hatchling dogfish emerge with numerous, well-formed dermal denticles (Ford 1921). Their teeth are small relative to their body size, and tooth morphology suggests they are used primarily for prey grasping rather than shearing (Moss 1977). In the light of these morphological traits, at a functional level the scale-rasping behaviour we observed may increase the food species available to juveniles in the wild (e.g. crustaceans, polychaetes), so could be ecologically important for expanding dietary breadth and increasing growth potential during early life. Interestingly, we have also observed the behaviour, albeit rarely, in adult *S. canicula* indicating that the pattern is not lost with maturation ($n = 3$ events; 12 fishes in 48 feeding bouts). Dermal denticles in adults protrude further from the body surface in the lateral caudal-peduncle area compared with other body areas, perhaps as a result of hydrodynamic adaptations (Bone 1975; Reif & Dinkelacker 1982), but the relative extension of denticles is an order of magnitude smaller in adults than in juveniles (extension from body surface was 0.02% and 0.18% of body length, respectively). This difference predicts that food anchoring should be less successful in adults and may reflect the low observed frequency. However, scale rasping may also be less common in adults (body length of *ca.* 0.7 m) because they are not usually gape limited with respect to preferred prey species such as small-bodied crabs and prawns (Ellis *et al.* 1996). Clearly, experiments are needed to determine the possible growth benefits of scale-rasping behaviour for juveniles.

Scale rasping in dogfish is convergent with aspects of behaviour in other gape-limited predators. Two species of

Table 1. Scanning electron microscopy measurements of dermal denticle length and vertical extension from the skin surface in three body regions of three dogfish aged between three and seven months.
(The mean was derived from measurements of five dermal denticles per image.)

		head		middle		caudal	
dogfish no. (body length, mm)		denticle length (mm)	denticle extension (mm)	denticle length (mm)	denticle extension (mm)	denticle length (mm)	denticle extension (mm)
1 (140)	mean	0.42	—	0.44	0.26	0.57	0.29
	s.d.	0.05	—	0.05	0.07	0.08	0.09
2 (166)	mean	0.34	0.19	0.35	0.17	0.43	0.15
	s.d.	0.02	0.07	0.03	0.08	0.06	0.02
3 (195)	mean	0.37	0.21	0.22	0.17	0.68	0.19
	s.d.	0.03	0.02	0.04	0.07	0.04	0.03

tropical snakes circumvent the constraints of oversized prey that they are unable to swallow whole, by removing each limb of large crabs that they subdue with body coils (Jayne *et al.* 2002). As with snakes, body-surface-facilitated feeding in dogfish is enabled partly owing to their elongated body morphology. Because *S. canicula* belongs to the most species-rich shark family, Scyliorhinidae (catsharks), scale rasping may be a common behaviour pattern among sharks generally. Scale-rasping behaviour could also occur in teleost fish, particularly in species with elongated bodies and prominent scales. Moreover, dermal denticles of thelodonts and shark-like fishes have been found in Ordovician deposits (Sansom *et al.* 1996) making them among the oldest known vertebrate fossils. This raises an interesting question about the age of scale-rasping behaviour: could early shark-like fishes have used dermal denticles to help tear prey into bite-sized pieces? The study of fossil fish morphology (dermal denticle, tooth and body shapes) may shed some light on this idea.

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